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MODELING OF COTTON INSECT POPULATIONS

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Western Region
Agricultural Research Service
UNITED STATES DEPARTMENT OF AGRICULTURE
In Cooperation With
Arizona Agricultural Experiment Station

MODELING OF COTTON INSECT POPULATIONS

By R. E. Fye[1]

INTRODUCTION

The increasing use of systems analysis to evaluate the biological facets of ecosystems requires that the entomologist quantitatively consider the many variables affecting the insect populations. Once he has basic data applicable to the various factors, he must organize these data into workable form. The technique best suited for this integration is modeling. Models may be broadly categorized into two groups—descriptive and predictive.

The descriptive model describes mathematically, or with simulation techniques, the processes associated with historical populations. Morris (*23*)[2] derived such models from life tables concerned with the spruce budworm, *Choristoneura fumiferana* (Clem.). Actually, a descriptive model becomes predictive if all possible situations have occurred while the data for the models were assembled. However, this goal is rarely achieved, and, by practical standards, a descriptive model cannot be considered a reliable predictive model.

THE PREDICTIVE MODEL

The intent of the predictive model is to forecast what will happen if certain simultaneous events occur. Since these events will have a historical background, it is necessary to consider a continuing sequence of these events. The best approach to the predictive model is the systems technique in which the various factors affecting populations are integrated into complex systems of difference or differential equations or other mathematical statements or into simulations which reflect the realistic systems that the predictive model intends to model. Probably one of the greatest pitfalls in which a neophyte modeler will indulge is the sifting of descriptive data in an effort to determine the factors affecting an insect population and to reorganize them into some predictive form. Generally, his efforts will result in futility. The predictive model is best based on data considering individual factors and precise experiments which answer simple questions regarding factors to be considered in the final model. It is also essential that the factors be integrated experimentally to determine which are critical interactions.

An overall predictive model must be considered as two major submodels. The first deals with the developmental facets of the insect population and answers the basic question, "When?" This submodel will reveal the stratification of age and stage within the subject insect populations, and, during most of the growing season, these strata are extremely dynamic. The second submodel deals with the natality and mortality that determine the numbers of insects in the population and answers the question, "How many?" The developmental submodel is relatively simple as compared to the natality-mortality submodel. Natality may be determined by utilizing the numbers of females in a population and their respective fecundity. The mortality portion requires a partitioning of the mortality among the various factors which may affect the population. These factors are frequently unrecognizable in the early parts of model development, and their elaboration after detection is a prime example of the utility of the systems approach in gaining insights into the population dynamics of insects.

The basic flow sheet describing the two submodels is presented in figure 1.

The Developmental Submodel

For the initiation of the developmental submodel in the spring, it is essential to understand the emergence of the overwintering segment of the prior year's populations. This will generally involve the triggering of diapause in the fall and the subsequent emergence of the diapausing individuals in the spring. In other instances, diapause may not be involved. In some cases, individuals may emerge before oviposition sites are available, and it is essential to have a population estimate either by model or by direct assessment when the oviposition sites do become available.

Much research has been directed toward the study of diapause, and adequate models are available to describe the entrance into winter hibernation by assessment of the factors triggering diapause. Although models to describe or predict the numbers of insects surviving the

[1] Research entomologist, Southern Arizona–New Mexico Area, Western Region, Agricultural Research Service, U.S. Department of Agriculture, Tucson, Ariz.

[2] Italic numbers in parentheses refer to Literature Cited, p. 5.

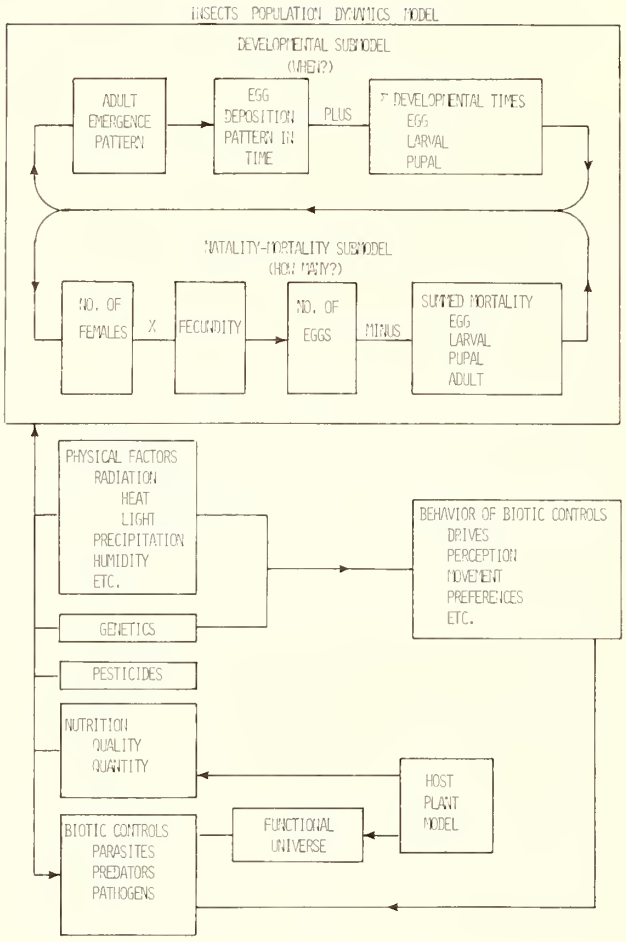

FIGURE 1.—Flow chart for the basic developmental and mortality submodels with the associated contributing factors.

winter, the triggering of emergence, and the population emergence patterns have been attempted, the models are not adequately developed (Fye and Carranza *16*). Therefore, it is necessary to assess the population directly at the time that oviposition sites become available. Many methods are available, but the assessment is complicated by the variance associated with sample means (Kuehl and Fye *22*; and unpublished data, 1973) and by the lack of adequate methods to assess the populations of mobile adult insects.

Although difficult to determine, the keys to the initiation of modeling the seasonal activities of insects are accurate assessments of the overwintering population, the fecundity of its females, and the emergence and oviposition patterns. Once the initial population and the oviposition pattern are determined, the subsequent development of the individuals can be estimated through the utilization of the proportion of development in a given period at a given temperature, that is, a physiological unit. Such systems have been described by Fye et al. (*10*), Fye and Bonham (*14*), and Fye and McAda (*17*) for several cotton insects in Arizona. These systems utilize the linear portion of the classical developmental curve (figure 2) relating development to temperature and must be reconciled when the temperatures leave the linear portion of the curve.

In the systems noted above, a 2-hour period was chosen so that the effects of changing temperatures during a 24-hour period could be elaborated. First, the proportion of development at a given temperature in a 2-hour period was determined with the reciprocal of the total developmental period. The regression line shown as part of the developmental curve in figure 2 was developed, and from this line, and/or its attending equation, the proportion of development at a given temperature for a 2-hour period was determined. For changing temperatures, the day is broken down into 2-hour periods and the mean temperature of each period determined. The proportions of the development for each 2-hour period are derived and summed. When the sum reaches 1, one-half of the population will have passed through the stage under consideration. Properly manipulated, the system can be utilized to determine the age stratification in the population at any time. In practice, the regression line for the rate of development of eggs is used to determine the time of egg hatch (figure 3*a*). Then, all individuals hatching during each day (the daily cohort) are subsequently subjected to developmental estimation by the use of the larval-pupal reciprocal units until such time as they become adults.

Because all insects in a population do not develop at the same rate (fig. 3*a* and *b*), it is essential to consider the differences as development and emergence proceed. The difference in the rate of development is probably determined genetically, and it is desirable to have strong population genetic data based on a wild population to estimate the differences in the developmental model. Because the spread of the differences in developmental rate is rather large, it is a prime factor in determining the overlap of generations and the timing of peaks of populations as the season progresses.

Once the adults have emerged, the oviposition pattern of the population must be known so that the eggs for the next generation can be deposited in the proper quantitative sequence in the model. Preliminary data for the pink bollworm are presented in figure 3*c*.

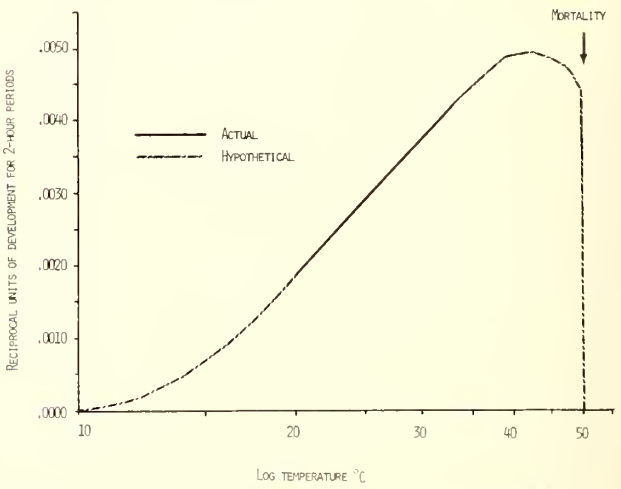

FIGURE 2.—Basic physiological rate curve for *Heliothis zea*, with reciprocal units of development for 2-hour periods on the X-axis.

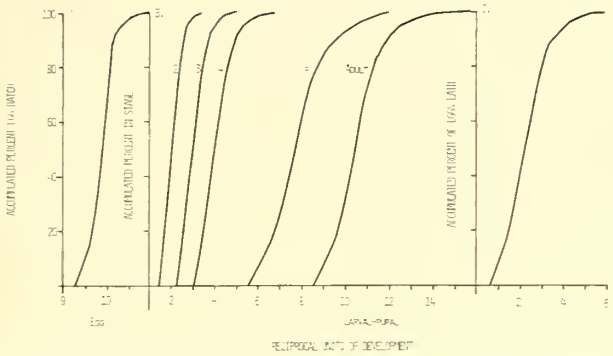

FIGURE 3.—The life cycle of the pink bollworm, *Pectinophora gossypiella* (Saunders), with (*A*) the accumulated egg hatch associated with the reciprocal units of development for eggs, (*B*) the subsequent development of the pink bollworm through the larval (instars 1, 2, 3, 4) and pupal (*P*) periods associated with the accumulated larval-pupal reciprocal units of development, and (*C*) the accumulated percentage of eggs laid by a population of pink bollworm females emerging on a given day associated with larval-pupal reciprocal units of development. (The oviposition pattern is probably not fully determined by temperature; therefore, the above data are presented as an example rather than as a final curve.)

For the remainder of the growing season, the numbers of eggs laid, the pattern of the oviposition, and the development for each daily cohort of insects may be determined, and, by proper manipulation of the age stratification, the peaks of any given stage may be estimated. In the latter portion of the season, the segment of the population comprising the diapausing population must be determined, and at this point we return to the initiation point of the developmental submodel.

The model we have presented is based upon temperature input, and it is well known that in row crops or any other type of vegetation, the ambient air temperature may be modified considerably by the plant canopy. This applies not only to the feeding or oviposition substrate on a plant, but also to the pupation substrate (commonly the soil). These modifications of temperature in the feeding site and pupation site must be considered if the developmental model is to function properly. For this purpose, regressions of the temperatures in the various plant parts or in soils where insects function must be developed with air temperatures as the independent variable. Bonham and Fye (*1*), Foster and Fye (*3*), Fye and Bonham (*9*, *10*, *11*, *12*, *13*), Fye et al. (*15*), and Fye (*5*, *7*) have developed regression equations for the estimation of the modification of the air temperature by the site components in Arizona cotton. Again, broad variance was evident, and, although the standard errors of the means showed that the estimates were very good, the standard deviations indicated many outlying points where the temperatures might diverge considerably from an estimated value and thereby be of considerable biological importance. Perhaps in future simulations, a random generation of the temperature regime, utilizing the distribution of the estimated temperature around the mean, will facilitate realistic simulation with relatively simple computations.

The Natality-Mortality Submodel

The developmental submodel described above is relatively simple as compared to the natality-mortality submodel. We noted that natality may be determined by ascertaining the number of females present, their fecundity, and the oviposition pattern. The numbers of females present require either a model estimation or a direct assessment, both of which are extremely difficult to determine. The potential fecundity is determined genetically, but the full potential is rarely realized. In desert areas, high temperatures are known to reduce fecundity, fertility, and, in some cases, longevity (Fye and Poole (*19*) and Fye and McAda (*17*)). Temperature extremes, humidity deficiencies, and other physical factor extremes are suspected of interfering with normal mating behavior. In addition, nutritional deficiencies and other physiological abnormalities during development may seriously reduce the potential fecundity. Therefore, the effective fecundity of the female population is a difficult factor to determine.

The mortality must be partitioned and attributed to the proper factor for the mortality submodel. Many physical factors, particularly those associated with climate, may be responsible for large reductions in the insect populations. In addition to slowing development (Fye and McAda *17* and Fye et al. *10*), high temperatures will cause high mortality to eggs laid on plants (Fye and Surber *20*) and prepupae of insects, such as the pink bollworm, pupating in the soil (Fye *6*). Heavy rainfall may wash insects from the plant and trap them in the mud beneath the plant. Rainfall may also seal moths emerging from subsurface pupae in the soil (Fye *8*). In addition, many combinations of high temperatures and low humidities (Ellington *2*) affect the physiological aspects of the insects' behavior. Nonclimatic physical factors which may cause mortality include summer cultivation of agricultural crops (Fye, unpublished data, 1973) and the winter tillage including crop residue destruction, disking, and plowing (Noble *24* and Watson and Larsen *25*). One other major mortality factor is pesticide application which may remove large segments of insect populations in agricultural areas.

The three categories of biological mortality factors are parasites, predators, and pathogens. One of the benefits of models is the ability to superimpose models of populations of biological control agents upon models of pests and determine if the coincidence of the two is adequate for a potential control of a pest. However, the assessment of biological factors is very difficult because the developmental and natality-mortality submodels which we have noted apply not only to the pests but also to the biological control organisms.

Superimposed on the biology and population dynamics are the behavioral responses which introduce the most complex factors associated with model development. If the behavioral factors such as the basic hunger and sexual drives, the perception of the prey or host, the movement of the predator or parasite, the food preferences, and the ever-changing searching universe in which biological control organisms operate must be included in the model, it may become necessary to determine the activities of the predator-parasite at a very basic level. Holling (*21*) applied the term "component analysis" to the study of

these basic functions at the several levels which he considered necessary to adequately assess the behavioral patterns. Obviously, the biological-behavioral interactions are the most difficult to put on a usable basis for a model.

The major factors commonly associated with mortality have been noted briefly, but many exist in natural ecosystems, and the analysis and assessment of these factors will be necessary for each system modeled.

TESTING AND USING THE SUBMODELS

Once a submodel is developed, it should be tested in the real world, and this will probably prove difficult. The broad variance associated with the sample means of insect populations was noted above. Due to this variance, it is necessary to accept broad confidence intervals with population estimates (Kuehl and Fye *22*). This is a major difficulty in sampling field populations and relating them to the model estimates. Certain major adjustments are usually necessary for the extrapolation of the laboratory developmental submodel to field situations for additional elaboration. The individual fascinated by mathematics or computers will tend to make these adjustments by placing some coefficient in his model, which brings it into line with field information. This approach should be avoided at all cost because most adjustments should have a biological basis if they are to be valid. This, of course, does not preclude the use of techniques to improve the manipulation of the model in the computer.

The times of peaks of the population and the age stratification at any given stage of the population may be determined with the developmental submodel. It is a very useful tool when based upon adequate elaboration of simple factors into the complex situation. However, the magnitude of these population peaks is far more difficult to predict because of the many factors associated with natality and mortality. Hopefully, as the model is developed, the key factors associated with both development and mortality can be determined, and the measurements necessary to relate the model to the real world can be restricted to a minimal number.

Once the insect population models are developed, they must be interfaced with similar plant models if plant feeding insects are involved. Fortunately, the fundamental factor, heat, is common to both models as the basic function driving the model. Other common factors affect the insect and plant populations; however, due to the complexity of the variables which interact to determine the overall function of populations of insects and plants, the interactions and mutual impact of the insect and plant populations may be difficult to evaluate and model. Nevertheless, the importance of this interface, which in reality is the basis for economic thresholds, demands that the entomologist, agronomist, and physiologist combine their efforts to develop an effective model.

Regardless of the complexity associated with the development of models by combining major key factors, the approach will be far more productive than the eternal sifting of data collected on field populations. Attempts to associate the factors in an existing system around a given species to the population dynamics of that species are better approached from the simple to the complex.

Emigration or immigration must be considered in the population dynamics of an insect in a given area. In either case, it is essential to be aware that it has occurred, which is an exceedingly difficult task due to our lack of knowledge of the factors associated with the triggering of major movement of insect populations. Fye and Bonham (*11*) suggested that the boll weevil in South Carolina moved when the oviposition sites became limited. This is one example of the type of data necessary for the consideration of migration. Other data on insect movement, such as that described for the boll weevil by Fye (*4*), are hypothetical and inferential, and are not adequate to describe population changes due to migration, but do provide some insights as to how the movement of major segments of the populations may occur.

Advantages of Models

We have concerned ourselves with a discussion of the content necessary to develop models for population dynamics of insects. Let us now consider the advantages of such a model. First, the model can tell us when we may expect a certain event or events to occur in the population dynamics of the species. With such data, the timing of the introduction of biological organisms and other control methods can be improved. Eventually, but in the now distant future, such models may provide us with the predictive capability which many entomologists desire. These models may take the form of systems of mathematical statements, or they may be computer simulations which do not require mathematical statement but utilize a memory bank of the necessary data. Regardless of the approach taken in the final models, a great deal of research is now necessary to produce the quantity and quality of data necessary to develop the predictive models. By far, the greatest immediate advantage to the research entomologist is the demand of the model for an insight into the factors which affect an insect population. Through the insights developed from the model and the model development, the entomologist becomes more cognizant of the problems which confront him and is better able to cope with a recognized situation than some undefinable vagary.

Disadvantages of Models

Probably of more immediate concern to many research workers are the pitfalls which may be encountered in the development of models.

First, the overenthusiasm for predictive capability may be consuming. Although predictive capability is highly desirable, we do not at this time have adequate data to provide predictive capability except in very limited situations. It will probably be many years before the key factors associated with population dynamics can be fully elaborated and the interactions combined into

a workable predictive model. For example, currently we can only use normal meteorological data, but until long-range meteorological forecasts become a reality, the predictive capability of insect models based mainly on temperature, which reflects the modified basic energy input from solar radiation, will not be fully realized.

The second pitfall is the inadequacy of current experimental designs to produce the caliber of data required by model building. The high-impact pesticide effects, to which many entomologists in the United States are conditioned, have restricted the use of elaborate experimental designs by entomologists for an extended period. Until entomological research returns to the discipline of refined experimental design, our models will continue to lack the proper data to provide the desired sensitivity. A classic result of this limitation is our current use of the regression technique and other mean values in our models. The use of these central tendency data fails to reflect the full biological diversity of many populations, and, until such time as the biological diversity is incorporated into our models, they will not provide the kaleidoscope of the real world.

Probably the greatest deficiency at the present time is the lack of research in population genetics regarding the basic functions of insects. This research must be incorporated in simulation models. Until population genetics research is initiated and directed toward the factors closely tied to population dynamics, our models will be basically weak.

CONCLUSIONS

Regardless of the tool employed for the control of an insect population, the basic requirement is an understanding of population dynamics. For the sledge-hammer effects in the pesticide research era just past, the empirical approach to insect control was feasible. However, with the advent of increased use of biological controls dictated by the concern over pollution of our atmosphere by pesticides, the empirical approach and the relatively simple assessment techniques associated with it are totally inadequate. The use of models will provide the best designed field experiment with minimal guesswork, which is commonly rampant in empirical research. In addition, entomologists who gain insight by utilizing the modeling concept, orient themselves to the important facets and factors associated with the development of an insect population. The great advantage of the modeling approach is the absence of retrogression once the basic model is developed. With the improved experimental designs and more adequate data, the models are improved without discarding large segments of the data as is frequently necessary in the empirical approach. Therefore, research efforts become additive, and in some cases exponential, when properly developed data are incorporated into a model and the wasteful empirical approach is eliminated.

The basic advantages of modeling are deeper insight into the factors of population dynamics, thereby opening the potential for improved control measures, and the discipline of the scientist for the improvement of his experimental procedures. Until systems analysis modeling techniques are incorporated into our experimental approaches, we will lack the insights and practical designs to achieve the true potential of what we now term "pest management" in our total agricultural ecosystems.

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